EFFECTS OF ENRICHMENT ON REPRODUCTION IN THE OPPORTUNISTIC POLYCHAETE *STREBLOSPIO BENEDICTI* (WEBSTER): A MESOCOSM STUDY

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ABSTRACT

The influence of organic enrichment on growth and planktotrophic development of the spionid polychaete *Streblospio benedicti* Webster was examined in two mesocosm experiments conducted at the MERL facility, University of Rhode Island. Specimens of *S. benedicti* were collected and their reproductive traits monitored near the conclusion of a two-year eutrophication experiment, and in the middle of a sludge addition experiment. Nutrient (N, P, and Si) enrichments at $8\times$ and $32\times$ the average aerial input into Narragansett Bay, Rhode Island, resulted in increases in body length, segment number, and length per segment, and a doubling of brood size in *S. benedicti* females. These increases were substantially higher during May ($12°C$) than August ($20°C$). Enrichment effects were stronger in the $8\times$ than $32\times$ nutrient treatment. In the sewage sludge experiment body size increased 20% over control values at the highest ($8\times$) sludge treatment level (nitrogen loading equivalent to the $8\times$ nutrient treatment) but no significant increase was noted at the $4\times$ sludge level, which received half as much nitrogen as the $8\times$ sludge treatment. Mean brood size increased by a factor of 4.6 over controls in the $8\times$ sludge treatment and by a factor of 2.3 in the $4\times$ sludge treatment. Within the range of adult body sizes observed, brood size enhancement occurred independent of increased length or segment number in both nutrient and sludge enrichment treatments. The ability to translate elevated food supply directly into increased reproductive output may underly opportunistic dynamics in macrobenthos. Brood size enhancement of the magnitude observed probably contributes to the high *S. benedicti* densities found in polluted or organically enriched settings.

INTRODUCTION

Increased concern over pollution of harbors and bays during the 1960's and 1970's spawned interest in community structure and succession of estuarine macrofauna (reviewed in Pearson and Rosenberg, 1978). Many estuarine studies revealed life history characteristics and population dynamics in polychaetes, crustaceans, and bivalves which are defined as opportunistic (*e.g.*, Grassle and Grassle, 1974; McCall, 1975). Life history traits associated with opportunism in macrobenthos include small size, rapid colonization ability, short generation time, high reproductive rate (r), and high mortality rate (Grassle and Grassle, 1974). Brood protection is also a common feature among many opportunistic polychaetes, including *Capitella* spp., *Polydora ligni,* and *Streblospio benedicti* (Grassle and Grassle, 1974; Levin, 1984a), and among peracarid crustaceans (Barnes, 1980). However, not all opportunists brood young; the bivalve *Mulinia lateralis* has completely planktonic development (Chanley and Andrews, 1971).

Opportunistic species colonize and dominate benthic assemblages during or following bottom disturbances, such as those caused by release of sewage or industrial wastes (Reish, 1971; Boesch, 1973), dredging and spoil disposal (Oliver, 1979), nutrient additions and subsequent eutrophication (Nixon *et al.,* 1984), oil spills (Grassle and Grassle, 1974; Sanders *et al.,* 1980), or severe storms and hurricanes (Boesch *et al.,* 1976; Rhoads and Boyer, 1983). Biological disturbance of sediment, such as that caused by digging activities of crabs, bottom fish, rays, or whales may also lead to colonization and persistence of opportunistic taxa (Virnstein, 1977; Van Blaricom, 1982; Levin, 1984a, Oliver and Slattery, 1985).

Pearson and Rosenberg (1978) make a distinction between disturbance and enrichment opportunists. They cite *Capitella* spp., *Streblospio benedicti, Scolelepis fuliginosa,* and dorvilleids as examples of species which colonize disturbances specifically resulting from organic enrichment. Species in the genus *Streblospio,* common in North America and Europe, are often numerically dominant in polluted or enriched estuarine habitats. *S. benedicti* recruits are typically found in caged settlement containers which trap fine organic particulates. Densities of over 100,000 individuals/m^2 have been reported in settling containers and clearings exposed for 2 weeks (McCall, 1975; Virnstein, 1977; Levin, 1984a). Enhanced recruitment may have resulted from either active habitat selection or passive entrainment (Hannan, 1984).

Streblospio is not limited to enriched or disturbed habitats. *S. benedicti* has been reported from most of the shallow estuaries, marshes, and mudflats studied in the United States, with the exception of some in Washington and Hawaii (Levin, 1984b). This species is often a moderate component of the background community but population size can grow exponentially in response to disturbance. Similar behavior is documented for *Capitella* spp. and *Polydora ligni* (Pearson and Rosenberg, 1978).

The mechanisms underlying opportunistic responses are just now being investigated. High population growth rates are thought to derive from life history characteristics while high mortality rates have been attributed to competition from later stages (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978; Gallagher *et al.,* 1983; Gallagher, pers. comm.). The dynamics of *Capitella* sp. I fed Gerber's cereal, was studied in the laboratory by Chesney and Tenore (1985a, b). They observed high amplitude population fluctuations in the presence and absence of induced mortality (artificial predation) over 90 weeks. High mortality occurred and they concluded that *Capitella* sp. I was unlikely to achieve equilibrium dynamics on its own. Based on these observations Chesney (1985) suggests that inherent life history traits (*e.g.,* reproductive lags and a tendency to overshoot carrying capacity) rather than competition are probably responsible for population declines of opportunists observed during succession in soft sediments. However, the meiofaunal community present in these experiments (Alongi, 1985) was not considered in the interpretation of *Capitella* sp. I dynamics and may have influenced resource availability.

The ability to rapidly translate increases in food availability to increased reproductive output should lead to opportunistic population dynamics, particularly if offspring remain to further utilize the enhanced food supply. Production of more gametes and offspring, independent or instead of concomitant somatic growth (which uses energy and takes time), should also enhance rapid population growth in opportunists. Eckelbarger (in press) suggests that opportunism among polychaetes is limited to species with brief gametogenic cycles, which permit numerical response to specific conditions before those conditions disappear. Spionid and capitellid polychaetes can produce mature gametes only a few weeks after initiating gametogenesis (Eckelbarger, in press).

This paper examines the reproductive responses by *Streblospio benedicti* to different forms of organic enrichment. *S. benedicti* was studied in two experiments conducted

in mesocosms at the Marine Ecosystems Research Laboratory (MERL), University of Rhode Island. One was a eutrophication experiment involving nutrient additions, the other involved addition of secondary sewage sludge. In an earlier paper (Levin, 1984b) I suggested that the widespread success of *S. benedicti* may be attributable to the occurrence of both planktotrophic and lecithotrophic modes of development in this species. The research presented here considers only *S. benedicti* with planktotrophic development and examines the plasticity of reproductive traits, such as egg and brood sizes.

Streblospio benedicti *background*

Streblospio benedicti Webster (Spionidae) inhabits the upper 2–3 cm of muddy sediments and constructs ephemeral tubes of fine-grain particles. This species is both a suspension feeder and surface-deposit feeder on plankton, organic aggregates, and sediments. Rod-shaped fecal pellets are deposited outside the tube (Levin, 1981). *S. benedicti* exhibits both planktotrophic and lecithotrophic modes of development in North America, but only planktotrophic development has been reported for *S. benedicti* in Narragansett Bay and in the MERL tanks (Levin, 1984b., J. P. Grassle, pers. comm.). Oogenesis takes place in paired ovaries in anterior segments (Eckelbarger, 1980) and fertilized ova enter paired dorsal brood pouches where development proceeds. Larvae are brooded to a 3–5 setiger stage, approximately 220 μm in length. Following release from brood pouches larvae usually feed in the plankton for 10–21 days before settlement (Levin, 1984b). Females can release hundreds of planktotrophic larvae per brood (Levin, 1984b) and may produce as many as 14 broods in a lifetime (Levin, DePatra, and Creed, in prep.).

MATERIALS AND METHODS

Streblospio benedicti was sampled from the MERL mesocosms, located at the University of Rhode Island on the lower West Passage of Narragansett Bay, RI. Sampling was conducted on 12 May and 17 August 1983, towards the conclusion of a 2-year eutrophication experiment and on 26 July 1984 during a 3-month sewage sludge enrichment experiment. The design of the MERL mesocosms is described in Pilson *et al.* (1979). System-wide results of the first year of the eutrophication experiment are presented in Nixon *et al.* (1984) and preliminary results of the sludge experiment are described in Oviatt (1984). Methodology critical to this investigation will be reviewed here.

The MERL mesocosms were 5.5 m high cylindrical tanks (1.83 m diameter). The tanks received seawater from Narragansett Bay at a rate sufficient to completely replace the water every 27 days. The mesocosms were mixed four times a day with rotating plungers on a schedule designed to mimic tidal currents and to resuspend bottom sediments to similar levels as in the Bay. The walls of the tanks were brushed twice a week to prevent fouling. Each tank contained a tray 2.52 m^2 × 40 cm deep filled with sediments. These sediments were collected intact from Narragansett Bay (using a 0.25 m^2 box core) between 28 April and 8 May 1981 for the eutrophication experiment. Fresh sediments were collected from central Narragansett Bay in October 1983, prior to the start of the sludge experiment. On 7 June 1984, surface sediments (to 2 cm depth) were removed from all tanks to eliminate a bloom of the tunicate *Mogula manhattensis* and fresh sediments from the Bay were added. Narragansett Bay sediments were muddy, containing roughly 83% silt-clay at the collection site (Hunt and Smith, 1983). The dominant taxa in these sediments at the start of the eutrophication

experiment were the polychaetes *Mediomastus ambiseta, Polydora ligni, Streblospio benedicti*, and *Chaetozone* sp., and the bivalves *Nucula annulata* and *Yoldia limatula* (Grassle *et al.*, 1985).

Eutrophication experiment

The eutrophication experiment involved daily additions of inorganic nitrogen, phosphorus, and silicon (Molar ratio 12.80:1.00:0.91) at 1×, 2×, 4×, 8×, 16×, and 32× the average areal input (of sewage and runoff) to Narragansett Bay (Table I). Each of six tanks received a different enrichment level and three tanks remained as unenriched controls. Nutrient additions began on 1 June 1981 and continued daily through 26 September 1983. Specimens of *Streblospio benedicti* were collected from 2 control tanks (Nos. 5 and 8), the 8× enrichment tank (No. 1), and the 32× enrichment tank (No. 7) on 12 May and 17 August 1983, approximately 2 and $2\frac{1}{4}$ years from the start of the experiment. The *S. benedicti* adults collected must have entered the tank as larvae from Narragansett Bay or were produced by adults established within the tank sediments. They could not have been individuals collected directly from the bay at the start of the experiment, since the lifespan of *S. benedicti* is <12 months (Levin, DePatra, and Creed, in prep.). Average temperature in the MERL mesocosm tanks was 12–13°C in May 1983 and 20–21°C in August 1983. Because this large temperature difference could have significant effects on reproduction, I consider the two sampling dates to represent two temperature treatments rather than replicate samplings.

Streblospio benedicti was collected from the upper 4 cm of MERL tank sediments using 1″ diameter cylindrical cores (5.067 cm², n = 5 cores/tank on each sampling date). Sediments were sieved through a 500-μm screen and all *S. benedicti* were sorted live under a dissecting microscope. Stage of maturity and sex were noted for all specimens. Females brooding young were isolated in petri dishes, anesthetized in 5% $MgCl_2$, and the following reproductive traits were measured: length (mm), number of setigers, position of the first gametogenic setiger, number of ova/ovary, ovum diameter (μm), number of brood pouches, number of larvae/brood pouch, and number of larvae/brood.

TABLE I

Experimental enrichments in the MERL eutrophication and sewage sludge experiments

Eutrophication experiment 1 June 1981–26 September 1983

| Treatment level | Daily additions (millimoles/m²) | | |
	N	P	Si
0x	–	–	–
8x	23.04	1.798	1.643
32x	92.03	7.19	6.570

Sewage sludge experiment 18 June 1984–21 September 1984

| Treatment level | Daily additions (millimoles/m²) | | | |
	C	N	P	Si
0x	–	–	–	–
4x sludge	105	14.5	2.07	0.38
8x sludge	210	29.0	4.13	0.77

Sewage sludge experiment

The sewage sludge experiment consisted of seven treatments. Nutrients (N, P, and Si) were added daily to 3 tanks at 1×, 4×, and 8× enrichment levels, as in the eutrophication experiment. Primary and secondary sewage sludge from the Cranston, Rhode Island, Water Pollution Control Facility was added daily at 1×, 4×, and 8× levels to generate 3 treatments which received total nitrogen at loading rates equivalent to the nutrient treatments. Three unenriched tanks served as controls. The daily enrichments began on 12 June 1984 and were terminated on 22 September 1984. *Streblospio benedicti* was sampled in 2″ diameter cores (17.57 cm² × 4 cm deep) from the 4× and 8× nutrient tanks, the 4× and 8× sludge tanks, and 3 control tanks on 26 July 1984. Five to eleven cores were collected from each tank though time did not permit processing of all cores. Sediments were sieved and *S. benedicti* was sorted and measured as described for the eutrophication experiment. J. P. Grassle provided density data for *S. benedicti* collected the preceding day using 1″ diameter cores (5.067 cm² × 4 cm deep) and a 300-μm screen (Grassle and Grassle, 1984; Grassle *et al.*, 1985). Few reproductive *S. benedicti* were found in the 1984 nutrient enrichment tanks, so only the sludge enrichment and control treatments are considered here.

Statistical analyses

Statistical tests were carried out with SAS software (Ray, 1982). All analyses except for regressions of brood size on adult length and setiger number were performed on untransformed data. One-way ANOVAs were used to analyze effects of enrichment level on *S. benedicti* densities in the eutrophication and sludge experiments. A two-way ANOVA and a SNK *a posteriori* test were performed to evaluate effects of enrichment level and month on female length, segment number, the first gametogenic setiger, ovum diameter, and numbers of ova/ovary, paired brood pouches, larvae/brood pouch, and larvae/brood in the eutrophication experiment. Effects of sludge level on these same parameters were analyzed using a one-way ANOVA and SNK test. A comparison was made of all 9 enrichment treatments across experiments, (May 1983, August 1983, and July 1984) using a one-way ANOVA and a SNK test for each reproductive character. Data from the eutrophication and sludge experiments were combined to determine Pearson product-moment correlations between reproductive traits.

Brood size data from the eutrophication and sludge experiments were log transformed to satisfy least-squares assumptions prior to performing regressions of brood size on adult length and on setiger number. Homogeneity of variances was examined using F tests to compare error mean squares from regressions for individual treatments. No departures from homogeneity were observed within each experiment. Regressions of log brood size on both adult length and on setiger number were performed across enrichment levels (separately in the eutrophication and sludge experiments), allowing for different intercepts and slopes.

RESULTS

Eutrophication experiment

Streblospio benedicti densities in each enrichment treatment are shown in Table II for samples collected in May and August 1983. In May *S. benedicti* exhibited no density difference among enrichment levels ($F_{3,16} = 1.92$, $P > 0.05$). Mean densities in all treatments ranged from 2.8 to 9.6 individuals/5.07 cm² core (5,600 to 19,200

TABLE II

Density of Streblospio benedicti *in the MERL eutrophication experiment*

Food level	x̄ Density (#/core)	S.D.	n (# of cores)	Core size (cm²)	x̄ Density (#/m²)	% Females brooding
12 May 1983						
0x (Tank 5)	9.60	6.20	5	5.07	19,200	80
0x (Tank 8)	2.80	1.48	5	5.07	5,600	55
8x (Tank 1)	4.00	4.38	5	5.07	8,000	75
32x (Tank 7)	4.80	4.70	5	5.07	9,600	58
17 August 1985						
0x (Tank 5)	4.60	2.94	5	5.07	9,200	50
0x (Tank 8)	0.00	0.00	4	5.07	0,000	—
8x (Tank 1)	25.60	16.33	5	5.07	51,200	50
32x (Tank 7)	31.00	11.64	4	5.07	62,000	58

(Mesh size = 500 μm).
One-way ANOVA on density.
May: $F_{3,16}$ = 1.92, $P > 0.05$.
August: $F_{3,14}$ = 7.81, $P < 0.005$.

individuals/m²). Three months later, in August, the 8× and 32× enrichment tanks exhibited mean densities equivalent to 25.6 and 31.0 individuals/core respectively (51,200 and 62,000 individuals/m²). These values were significantly higher than control values in August, but not different from each other ($F_{3,14}$ = 7.81, $P < 0.005$). On both sampling dates at least 50% of the females collected in each treatment were brooding larvae (Table II).

The two control (0×) tanks, sampled in May, exhibited between-tank differences in number of ova/ovary (x̄ = 6.2 in tank 8 *vs.* x̄ = 4.2 in tank 5, one-way ANOVA, P = 0.007). However, there was no significant difference in brood size. May reproductive data from the two control tanks were pooled in analyses of enrichment level effects. Mean values of female reproductive traits are given for *S. benedicti* at 0×, 8×, and 32× enrichments in May and at 8× and 32× enrichments in August in Table III. Unfortunately, only two reproductive females were found in the control (0×) tanks in August, so analysis of food level effects for August does not include the 0× treatment.

During May, female body length was significantly greater in the 8× and 32× enrichment tanks than in the controls (P = 0.0087), but in both May and August, body length did not differ between the 8× and 32× treatments. The number of setigers was significantly greater in 8× than control treatments during May (P = 0.0304), but no difference in setiger number was observed between the 32× treatment and controls in May or between 8× and 32× treatments in both May and August. Between-month comparisons of body size, for 8× and 32× treatments, suggest that in August there was a decrease in body length (P = 0.0090) but no accompanying change in segment number (Table III, Fig. 1). Length per segment was greater in May than August in enriched tanks. Females sampled in August may have been younger, summer recruits, while the larger individuals sampled in May probably overwintered in the tanks.

As one trait responds to treatments other traits may be constrained to follow, thus correlations among reproductive characters must be considered in interpretation of treatment effects. Measures of body size (length and setiger number) were positively correlated with numbers of ova per ovary (r = .55 for length, r = .44 for setiger number), total number of paired brood pouches (r = .73, r = .82), number of larvae per brood pouch (r = .52, r = .36), and number of larvae per brood (r = .69, r = .61)

TABLE III

Reproductive traits of Streblospio benedicti *in the MERL eutrophication experiment*

	12 May 1983			17 August 1985		2-way ANOVA	
	0x	8x	32x	8x	32x		
	x̄ (S.D.)	x̄ (S.D.)	x̄ (S.D.)	x̄ (S.D.)	x̄ (S.D.)	Food	Month
Adult length (mm)	5.2 (1.4) n = 36	7.2 (1.9) n = 11	6.1 (1.6) n = 18	5.7 (1.2) n = 17	4.8 (1.0) n = 19	*P* = .0087	*P* = .0090
	b	a					
No. of setigers	42.6 (6.0) n = 35	49.4 (6.1) n = 12	46.2 (5.8) n = 18	45.4 (5.8) n = 17	41.6 (4.4) n = 19	*P* = .0304	NS
		a					
	b		b				
First gametogenic setiger	10.1 (0.6) n = 36	9.8 (0.8) n = 13	10.0 (0.6) n = 18	10.6 (1.1) n = 16	10.6 (0.8) n = 15	NS	NS
Ovum diameter (μm)	56.1 (23.2) n = 38	60.0 (21.7) n = 13	61.3 (27.3) n = 19	50.8 (18.3) n = 12	56.7 (19.5) n = 15	NS	NS
No. of ova/ovary	5.8 (1.9) n = 37	8.1 (2.8) n = 9	5.9 (1.9) n = 15	6.1 (1.9) n = 11	4.1 (1.0) n = 13	*P* = .0002	*P* = .0011
	b	a	b	a	b		
No. of paired brood pouches	9.0 (2.8) n = 37	14.0 (3.6) n = 13	11.8 (2.6) n = 17	9.2 (2.7) n = 17	9.5 (2.2) n = 17	NS	*P* = .0228*
	b		a	b	a		
No. of larvae/brood pouch	6.8 (2.3) n = 18	10.4 (3.4) n = 11	7.4 (1.7) n = 14	7.4 (1.6) n = 10	5.0 (1.4) n = 2	*P* = .0011	*P* = .0021
	b	a	b				
No. of larvae/brood	103.9 (54.7) n = 28	278.2 (143.3) n = 13	184.3 (90.1) n = 15	131.6 (45.6) n = 14	67.6 (41.7) n = 21	*P* = .0001	*P* = .0002
		a		a	b		
	b		b				

* Significant food-month interaction *P* = .0177.
(Lines show differences among means analyzed for each month separately.)
NS = not significant.

(Table IV). These correlations suggest that changes in body size may also lead to changes in fecundity. Numbers of ova and larvae were also highly correlated with one another (r = .61), thus we might expect to see them respond in identical fashion to food and temperature (month) treatments. Body size was not correlated with egg size or with position of the first gametogenic setiger (Table IV).

Both enrichment level and month (temperature) had significant effects on ovum number (*P* = 0.0002 for food, *P* = 0.0011 for month), numbers of larvae per brood pouch (*P* = 0.0011, *P* = 0.0021) and brood size (*P* = 0.0001, *P* = 0.0002) (Table III). Ovum size and position of the 1st gametogenic setiger were unaffected (Table III). During May the mean number of larvae produced per brood was 167% higher than
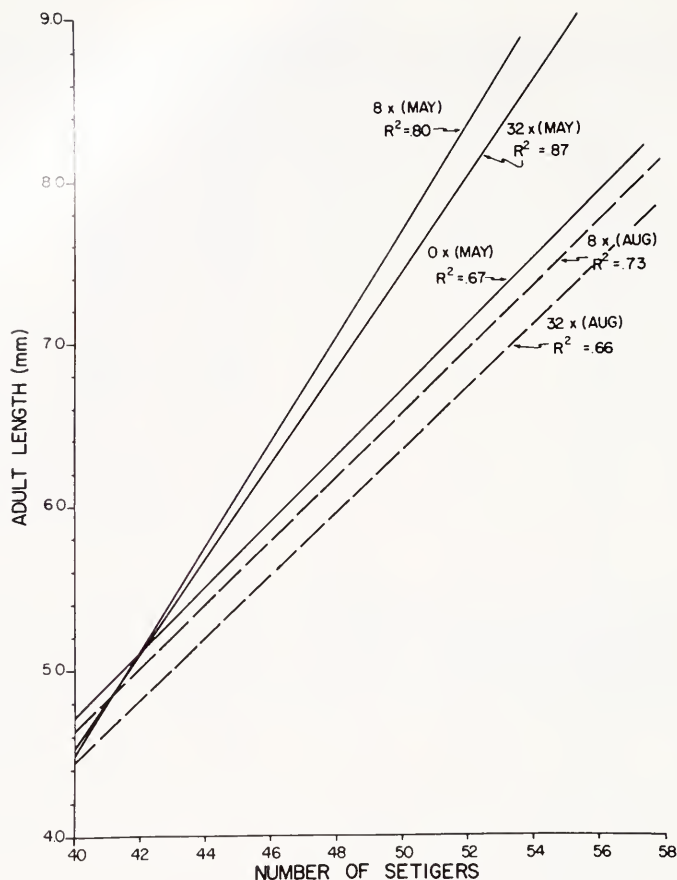
FIGURE 1.   Least-square regression of *Streblospio benedicti* segment number on length in the MERL eutrophication experiment.——May 1983; - - - - - August 1983.

$$\text{May } 0\times \text{(control): } y = -3.11 + 0.196x \quad P < .0001$$
$$8\times \quad : y = -6.59 + 0.277x \quad P < .0001$$
$$32\times \quad : y = -5.65 + 0.255x \quad P < .0001$$
$$\text{August } 8\times \quad : y = 2.65 + 0.183x \quad P < .0001$$
$$32\times \quad : y = 2.99 + 0.187x \quad P < .0001$$

Slopes for May 8× and 32× treatments differ significantly from the others.

the controls ($\bar{x}$ = 104) in the 8× enrichment ($\bar{x}$ = 278) and 77% higher than the controls in the 32× enrichment ($\bar{x}$ = 184). However, only the 8× and 0× treatments differed significantly from one another ($P = 0.0001$). Seven females produced broods > 300 larvae (the largest was 548); all were large individuals from enriched treatments.

Brood size was highly correlated with adult length (r = .69, $P < 0.0001$) and segment number (r = .61, $P < 0.0001$). Scatter plots of May brood sizes as a function of length and setiger number are given for each enrichment level in Figures 2a and b. Although correlation does not necessarily indicate a causal relationship, the well known

TABLE IV

Correlation coefficients of Streblospio benedicti *reproductive traits in the MERL eutrophication and sludge experiments combined*

	Adult length	No. of setigers	First gametogenic setiger	Ovum diameter	No. of ova/ovary	No. of paired brood pouches	No. of larvae/brood pouch	No. of larvae/brood
Adult length	1.0	.86	NS	NS	.55	.73	.52	.69
No. of setigers		1.0	NS	NS	.44	.82	.36	.61
First gametogenic setiger			1.0	NS	−.20	NS	NS	−.21
Ovum diameter				1.0	.21	NS	NS	NS
No. of ova/ovary					1.0	.40	.54	.61
No. of paired brood pouches						1.0	.50	.70
No. of larvae/brood pouch							1.0	.71
No. of larvae/brood								1.0

All values are significant at $P < .05$.
NS = not significant.

association between body size and fecundity raises the possibility that the increases in brood size observed in May enrichment treatments (8× and 32×) resulted solely from increases in body size. To examine this possibility, log brood size was regressed on both adult length and on setiger number, across enrichment levels. Both regressions yielded r^2 values > 0.995. Tests for differences among slopes across enrichment levels were significant ($P < 0.0001$) for regressions of log brood size on setiger number ($F_{3,46}$ = 24.5) and length ($F_{3,47}$ = 23.5). However, fitted lines for the three enrichment levels did not intersect within the range of observed setiger numbers (8× values > 32× > 0×). The 0× and 32× treatment lines crossed only at the very largest adult lengths observed. Predicted brood sizes for the 8× treatment were greater than those for the 0× and 32× treatments within the entire range of body sizes observed. Thus, though the regression lines for each enrichment level were not parallel, their intersection took place at biologically meaningless (unrealistically large) body and brood sizes.

A between-month comparison shows significantly ($P = 0.0002$) smaller broods were produced in August (Table III, Fig. 3). Brood sizes were less than half those observed in May; mean brood size was 132 for the 8× treatment and 68 for the 32× treatment.

Sewage sludge experiment

The mean density of *S. benedicti* was considerably lower in the control (0× enrichment) tanks [x̄ = 4.63 individuals/17 cm² core (2,635/m²)] than in the 4× sludge treatment [x̄ = 60 individuals/core (34,140/m²)] or the 8× sludge treatment [x̄ = 22 individuals/core (12,515/m²)] ($F_{4,10}$ = 17.01, $P < 0.001$) on 26 July 1984, one month into the sewage experiment (Table V). Density estimates based on two 1″ cores per tank provided by J. P. Grassle were 4–5 times higher than those from the 2″ diameter cores (due to use of a finer mesh for processing sediment), but yielded consistent differences among treatments (Table V). One control tank (No. 3) produced all except one of the control females brooding young. Fifty-five percent of females were brooding in that control tank, 88% were brooding in the 4× sludge treatment, and 85% were brooding in the 8× sludge treatment (Table V).
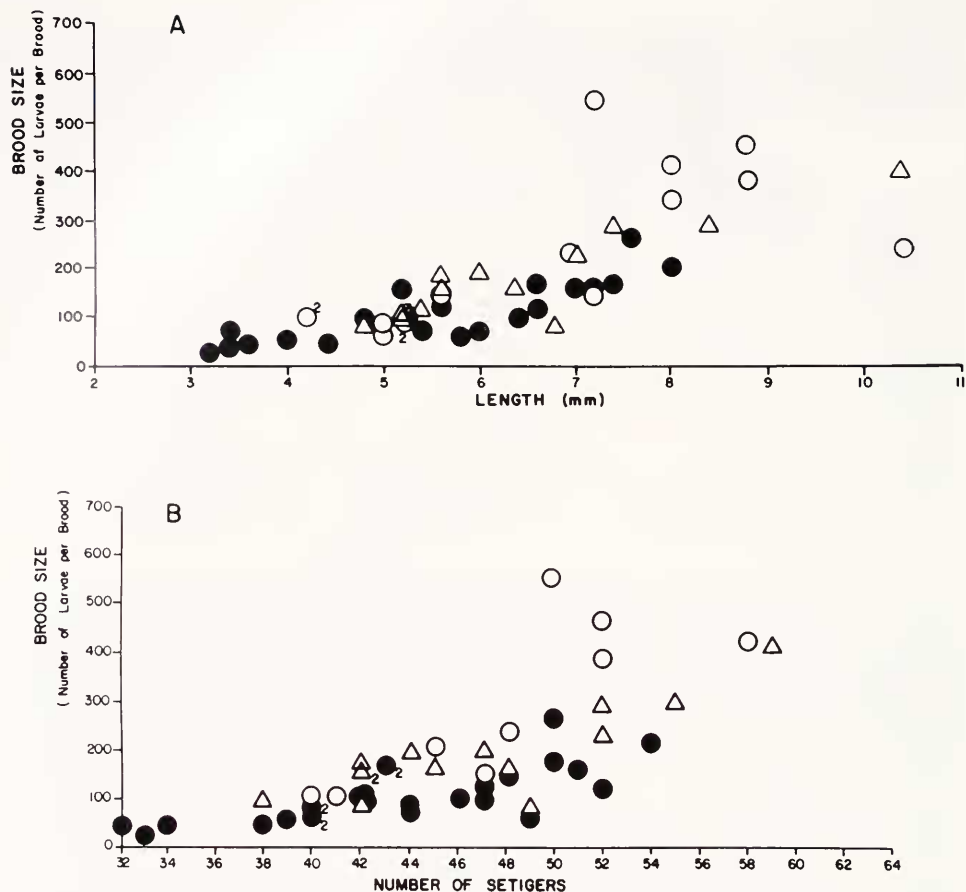
FIGURE 2. *Streblospio benedicti* brood size as a function of: A) length and B) setiger number in the MERL eutrophication experiment, 12 May 1983. ● = controls (Tanks 5 and 8); ○ = 8× enrichment (Tank 1); △ = 32× enrichment (Tank 7).

Evaluation of enrichment level effects on female traits indicate that female length ($P = 0.0319$) and number of setigers ($P = 0.0244$) were significantly greater in the 8× sludge treatment than in the 4× and 0× treatments, which did not differ from one another (Table VI). Females in the 8× sludge treatment also produced more ova/ovary ($P = 0.0002$), more larvae per brood pouch ($P = 0.0005$), and more larvae per brood ($P = 0.0001$) than the other two treatments, which did not differ significantly from one another (Table VI). Mean brood size in the 8× sludge treatment ($\bar{x} = 462$) was almost twice that of the 4× sludge tank ($\bar{x} = 235$) and over 4 times that of the controls ($\bar{x} = 100$). The only trait for which the 4× sludge treatment differed from the control was in the total number of paired brood pouches ($P = 0.0004$). As in the eutrophication experiment, position of the first gametogenic segment and ovum size were not affected by sludge level.

A scatter plot of brood size as a function of length (Fig. 4a) and segment number (Fig. 4b) for each sludge enrichment level reveals an exponential increase in brood size with body size. Five individuals in the 8× sludge treatment produced over 500
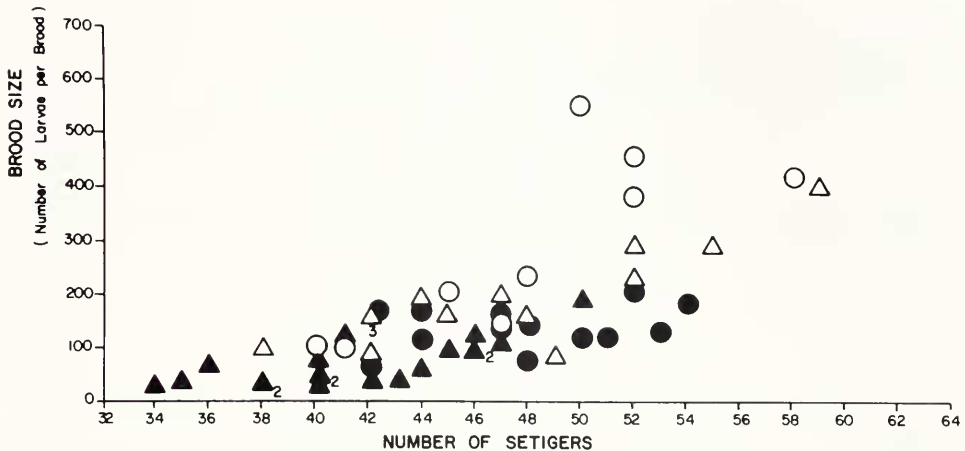
FIGURE 3. *Streblospio benedicti* brood size as a function of setiger number in the enriched treatments of the MERL eutrophication experiment. 12 May 1983: $\bigcirc$ = 8× enrichment, $\triangle$ = 32× enrichment. 17 August 1983: $\bullet$ = 8× enrichment, $\blacktriangle$ = 32× enrichment. The numbers indicate identical data points.

larvae/brood (Fig. 4). The maximum brood size observed, 1058, far surpassed any values reported for *S. benedicti* in a laboratory or field situation. Regressions of log brood size on adult length and on setiger number, across sludge enrichment levels, yielded r^2 values > 0.994. Tests for differences among slopes across sludge levels were significant for regressions of log brood size on setiger number ($F_{3,35}$ = 14.59, P < 0.0001) and on length ($F_{3,36}$ = 20.50, P < 0.0001). However, fitted lines for the three sludge levels did not intersect within the range of observed adult segment numbers or body lengths. For all sizes of worms capable of reproducing, predicted brood sizes were greater in the 8× sludge treatment than in the 4× sludge treatment, and both were greater than those in the 0× sludge treatment.

TABLE V

Density of Streblospio benedicti *in the MERL sewage sludge experiment (26 July 1984)*

Food level	x̄ Density (#/core)	S.D.	n (# of cores)	x̄ Density (#/m²)	% Females brooding
0x (Tank 3)	5.64 (4.0)	2.90	11 (2)	3,209 (7,905)	55
0x (Tank 5)	3.00 (4.0)	1.41	3 (2)	1,707 (7,905)	No mature females
0x (Tank 8)	1.50 (4.5)	1.50	2 (2)	854 (8,893)	100 (one mature female)
4x (Tank 6)	>60.00 (84.0)	—	1 (2)	>34,140 (165,019)	88
8x (Tank 2)	22.00 (25.0)	10.42	4 (2)	12,518 (49,407)	85

( )—indicates data from two cores/tank collected on 25 July 1984 by J. P. Grassle. Screen Size = 300 μm; Core Size = 5.07 cm².
(Screen Size = 500 μm, Core Size = 17.57 cm²); One-way ANOVA on density: $F_{4,10}$ = 17.01, P < 0.001.

TABLE VI

Reproductive traits of S. benedicti *in the MERL sludge experiment 26 July 1984*

| | Sludge enrichment level | | | One-way ANOVA | |
| | 0x | 4x | 8x | | |
	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)	$\bar{x}$ (S.D.)		P
Adult length (mm)	5.3 (1.4) n = 11	5.8 (1.0) n = 19	6.8 (2.0) n = 14	$F_{2,41} = 3.75$	.0319
No. of setigers	41.4 (5.5) n = 11	45.4 (4.8) n = 18	47.9 (6.7) n = 14	$F_{2,40} = 4.08$	.0244
First gametogenic setiger	9.3 (0.7) n = 12	9.6 (0.5) n = 18	9.5 (0.9) n = 13	$F_{2,40} = 0.39$	NS
Ovum diameter (μm)	60.9 (25.0) n = 11	55.0 (23.6) n = 17	58.6 (23.8) n = 14	$F_{2,39} = 0.21$	NS
No. of ova/ovary	6.2 (1.3) n = 11	5.4 (1.7) n = 16	8.4 (3.0) n = 13	$F_{2,37} = 7.14$	.0002
No. of paired brood pouches	9.0 (2.6) n = 12	12.4 (3.3) n = 19	14.3 (3.3) n = 14	$F_{2,42} = 9.44$	.0004
No. of larvae/brood pouch	7.1 (1.7) n = 12	9.0 (1.4) n = 10	11.7 (3.7) n = 13	$F_{2,32} = 9.86$	.0005
No. of larvae/brood	100.0 (54.0) n = 11	235.1 (107.1) n = 19	462.8 (296.4) n = 13	$F_{2,40} = 12.78$	.0001

Lines show significant differences among means.
NS = not significant.

Comparison of the eutrophication and sewage sludge experiments

A comparison was made of all nine treatments (3 nutrient levels in May 1983, 2 nutrient levels in August 1983, and 3 sludge levels in July 1984) for each reproductive character (Table VII). May 1983 and July 1984 unenriched controls showed no significant difference in any trait except position of the first gametogenic setiger (Table VII). *S. benedicti* from the 8× nutrient addition in May 1983, were most similar to the 8× sludge addition in July 1984. These treatments produced adults which were significantly longer, had more segments, more brood pouches, and greater brood size than the May 1983 and July 1984 controls. The 4× sludge treatment and May 32× nutrient addition generally exhibited the next highest values for these traits, but did not always differ significantly from control values. Females produced significantly larger broods in the 8× sludge treatment than in any other treatment.

DISCUSSION

The sacrifice of replication for an increased number of treatments seems to be a common difficulty in the design of mesocosm and other large-scale experiments (see
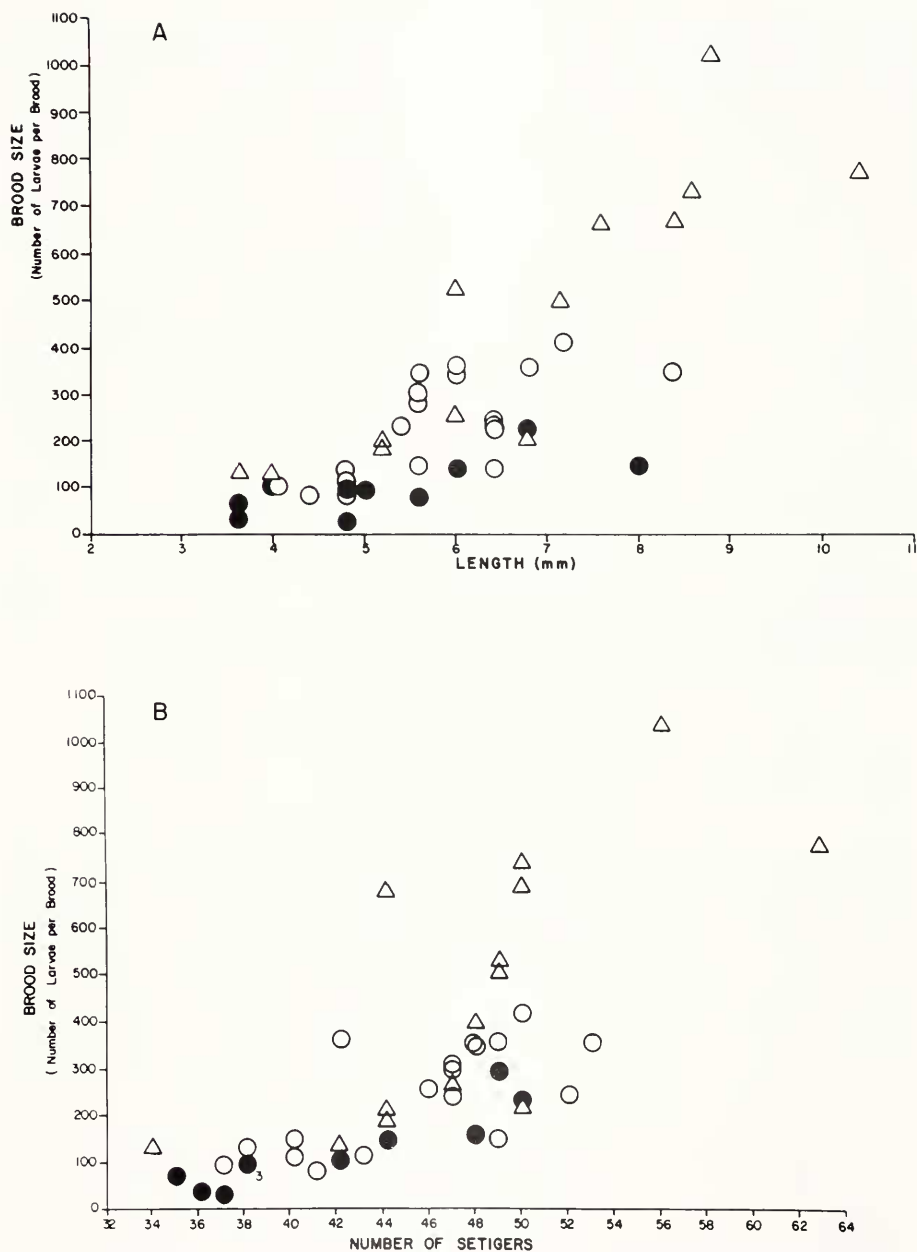
FIGURE 4. *Streblospio benedicti* brood size as a function of: A) length and B) setiger number in the MERL sewage sludge experiment. 26 July 1984. ● = O× control (Tank 3); ○ = 4× sludge addition (Tank 6); △ = 8× sludge addition (Tank 2).

Hurlbert, 1984; Smith *et al.,* 1984 for discussion). The lack of tank replication of enrichment treatments in both the MERL nutrient and sewage experiments must temper the interpretation of the data. The fact that the control (0×) tanks behaved

TABLE VII

Comparison of Streblospio benedicti *reproductive traits among all MERL treatments*

1. = 0x Nutrients	May '83
2. = 8x Nutrients	May '83
3. = 32x Nutrients	May '83
4. = 8x Nutrients	August '83
5. = 32x Nutrients	August '83
6. = 0x Sludge	July '84
7. = 4x Sludge	July '84
8. = 8x Sludge	July '84

	One-way ANOVA	Student-Neumann-Keuls Test
Adult length	$F_{7,137} = 4.97, P = .0001$	2 8 3 7 4 6 1 5
No. of setigers	$F_{7,136} = 4.04, P = .0005$	2 8 3 7 4 1 5 6
First gametogenic setiger	$F_{7,133} = 6.39, P = .0001$	5 4 1 3 2 7 8 6
Ovum diameter (μm)	$F_{7,131} = 0.32, P = NS$	3 6 2 8 5 1 7 4
No. of ova/ovary	$F_{7,117} = 6.19, P = .0001$	8 2 4 6 3 1 7 5
No. of paired brood pouches	$F_{7,138} = 10.10, P = .0001$	8 2 7 3 5 4 1 6
No. of larvae/brood pouch	$F_{7,82} = 7.12, P = .0001$	8 2 7 3 4 6 1 5
No. of larvae/brood	$F_{7,126} = 17.61, P = .0001$	8 2 7 3 4 1 6 5

NS = not significant.

similarly lends little confidence that single tanks are an adequate reflection of all possible outcomes of particular levels of enrichment. Each treatment exhibited its own benthic dynamics throughout the experiments. Some tanks evolved oxygen stress in response to nutrient loadings or high densities of competitors or predators while others did not (J. P. Grassle, pers. comm.; Frithsen *et al.,* 1985). Within a treatment, macrofaunal community composition varied greatly from year to year (Frithsen *et al.,* 1985). However, several benthic species exhibited essentially linear responses to level of nutrient additions after the first summer of the eutrophication experiment (Grassle and Grassle, 1984; Grassle *et al.,* 1985).

To understand responses of *S. benedicti* it is necessary to consider both biotic and abiotic influences on reproduction. During the eutrophication experiment in both May and August 1983, the length, segment number, egg production, and brood size of *S. benedicti* in the 32× enrichment treatment fell below those of the 8× enrichment tank (Table III). Despite a four-fold increase in nutrient loading, it appears that *S. benedicti* did not respond in the 32× treatment. Intraspecific competition has been shown to influence somatic growth and reproductive allocation in benthic invertebrates (Peterson, 1982; Zajac, 1985). However, there was no detectable difference between *S. benedicti* densities in the 8× and 32× treatments throughout the spring and summer of 1983 (Table II, J. P. Grassle, pers. comm.; J. Frithsen, pers. comm.). The density of *Polydora ligni,* a potential competitor, was extremely high in the 32× treatment during that period. *P. ligni* abundance was 5.7 times higher than *S. benedicti* in April (x̄ = 56,246 *vs.* 9,868/m²), 10.6 times higher in May (x̄ = 114,860 *vs.* 10,854/m²), 8.7

times higher in June ($\bar{x}$ = 186,698 *vs.* 21,512/m^2), and 4.2× higher in July ($\bar{x}$ = 262,482 *vs.* 62,167/m^2). *P. ligni* densities were consistently lower than *S. benedicti* in the 8× enrichment tank during those months (J. P. Grassle, pers. comm.; J. Frithsen, pers. comm.). The 32× enrichment tank experienced anoxic conditions between 29 July and 3 August 1983 (Frithsen *et al.*, 1985). *P. ligni* densities in this tank declined. Following this event, *S. benedicti* increased to 346,359 individuals/m^2 by September, the highest density observed for this species during the 3-year experiment. *Mulinia lateralis* was consistently abundant in this treatment throughout the summer and fall of 1983 (Frithsen, pers. comm.).

P. ligni and *S. benedicti* were among the species which demonstrated the greatest numerical response to nutrient enrichment in 1983 and sewage enrichment in 1984. Both species filter organic particles from the water column and feed on surface deposits. Frithsen and Doering (submitted) showed that these two species can increase net sedimentation when they reach high abundances. *P. ligni* is larger than *S. benedicti*, has longer palps (pers. obs.), is more aggressive (Levin, 1981; Whitlatch, pers. comm.), and could easily outcompete *S. benedicti* for food at the densities observed in the 32× enrichment tank. These interactions may have contributed to the small size and lower fecundity exhibited by *S. benedicti* in the 32× treatment relative to the 8× enrichment. In addition, oxygen stress might have produced decreases in reproductive output. A similar anoxic event occurred in mid September, 1984, when the 8× sludge treatment went anoxic and all benthos died. Just prior to the anoxia *S. benedicti* had been the numerical dominant. Unfortunately, no reproductive data were collected at that time.

Temperature may influence the magnitude of the reproductive response given by *S. benedicti* to organic enrichment. At low temperatures in May 1983 (12°C), increased food supply led to increases in size of reproducing females (Fig. 1) and to increased brood size independent of body size (Figs. 2a, b). In August, when temperatures had risen to 20°C, enrichment effects were reflected in level of reproductive activity. Few or no reproductive females were collected in control tanks. In the 8× and 32× enrichments, reproductive activity was high but body size and brood size were comparable to May control levels (Table II). Younger ages of females, due to recruitment during the summer, and response to increased metabolic demands at higher temperature or lower oxygen levels, may have been responsible. In addition, six- to seven-fold increases in *S. benedicti* density (Table II) may have intensified intraspecific competition and resulted in lower brood sizes than observed in May. In laboratory manipulations of temperature and food regimes, Levin and Creed (in press) found that body size and brood size of North Carolina *S. benedicti* with planktotrophic development increased in response to cooler temperatures. In that study food level had no effect on quantitative reproductive characters but lower food levels decreased the proportion of females which reproduced. The experiment did not examine competition for food.

S. benedicti appears to have the ability to translate enhanced food supplies directly into increased reproductive output. Utilization of heterosynthetic yolk sources during vitellogenesis, by sequestering materials from the circulatory system (Eckelbarger, 1980), may be one means by which *S. benedicti* can transfer food rapidly and directly into eggs and offspring. This capability may be essential to opportunists which depend on ephemeral resources and which, through utilization of these resources, may even contribute to their own demise. *S. benedicti* with planktotrophic development mature rapidly. They disperse their young during a 10–21 day larval planktonic phase (Levin, 1984b) and thus are not dependent on temporal persistence of a specific habitat.

Food quality, particularly nitrogen content, may regulate polychaete growth and reproduction (Tenore, 1977; Tenore and Chesney, 1985). Nutrient addition treatments in the eutrophication experiment and sewage treatments in the sludge experiment

exhibited elevated chlorophyll levels, and enhanced phytoplankton concentrations (Nixon *et al.,* 1984; J. Maugham, pers. comm.). The combination of sewage sludge and a rich phytoplankton supply clearly represents a high quality food source for *S. benedicti.* The 2–5-fold increases in brood size exhibited in the 8× and 4× sludge tanks (relative to controls) far surpass the increases observed in the nutrient enrichment treatments the previous year. In studies of the benthic dynamics in the nutrient and sludge treatments during summer 1984, Maughan (in prep.) found that *S. benedicti* densities increased in the sludge treatments but not in the nutrient treatments. Phytoplankton production was also lower in the nutrient treatments during summer 1984 and Maughan (in prep.) suggests that filtering activities of the abundant amphipods, molluscs, and polychaetes in these tanks were responsible. By August 1984 *S. benedicti* had also attained very high densities in the 1× sewage treatment (J. Maugham, in prep.). Percent organic carbon in the top cm of sediment of the 1×, 4×, and 8× sludge treatments during August (3.58, 2.52, and 2.92, respectively) was higher than in control tanks (2.16–2.26) or the 1×, 4×, and 8× nutrient treatments (2.05, 2.19, and 2.58, respectively). These data suggest that at equivalent loadings, the sewage yielded more food for deposit feeders than the nutrient additions. Other constituents of the sewage sludge, which were not present in the nutrient addition tanks, may have stimulated recruitment, growth, or reproduction in *S. benedicti.*

Streblospio benedicti response to organic enrichment in the form of rapid, large increases in brood size is not surprising, and may demonstrate one reproductive tactic underlying opportunistic population dynamics. The calanoid copepods *Acartia tonsa* and *A. hudsonica* responded to nutrient enrichments with increases in daily egg production, maximum length and dry weight (Sullivan and Ritacco, 1985). However, these increases were often not reflected in zooplankton abundance while increased brood size in *S. benedicti* was accompanied by elevated benthic densities. The polychaete response to food may also explain why we often see strong seasonal cycles in *S. benedicti* populations which actively reproduce all year (*e.g.,* Levin, 1984a). Increases in brood size during periods of increased food availability or cooling temperatures (Levin and Creed, in press) may cause dramatic recruitment peaks. It is not known whether the increased brood size exhibited by the small individuals in the sewage sludge tanks were accompanied by a decrease in reproductive output later in life. Release of larvae earlier rather than later in life is certainly adaptive for an opportunistic species. More work is needed to determine exactly what triggers population explosions in opportunistic species and how these explosions are achieved. In the case of enrichment opportunists such as *S. benedicti,* organic particulates are rapidly converted into both somatic tissue and offspring and order of magnitude increases in larval production may result.

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